

The University of Chicago

THE ANATOMY OF THE ROOT OF
SAGITTARIA LATIFOLIA

A DISSERTATION SUBMITTED TO THE
GRADUATE FACULTY IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

By
CHARLES FRANCIS SEVERIN

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ORIGIN AND STRUCTURE OF THE SECONDARY ROOT OF SAGITTARIA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 430

CHARLES F. SEVERIN

(WITH TWENTY FIGURES)

The origin of root structures appears to have been determined so definitely by past investigators that apparently there is little need to reinvestigate this region. It would seem advisable, however, to check their work from time to time, to see whether the present technique and point of view can both confirm the earlier findings and add details. This paper, therefore, is the result of a check on the work of JANCZEWSKI (1, 2) with the roots of plants. While several forms have been studied, only the results obtained with the various forms of *Sagittaria latifolia* are here described.

Since mitotic figures seemed necessary in tracing cell generations, the time of collecting and killing the specimens was varied. Roots killed about noon gave the maximum number of figures. Various killing reagents were used. Chromo-acetic 1 per cent and formalin 4 per cent plus alcohol 60 per cent gave good results, while Carnoy's solution blasted the tissue, and Flemming's, medium and weak, did not give results superior enough to justify the extra trouble.

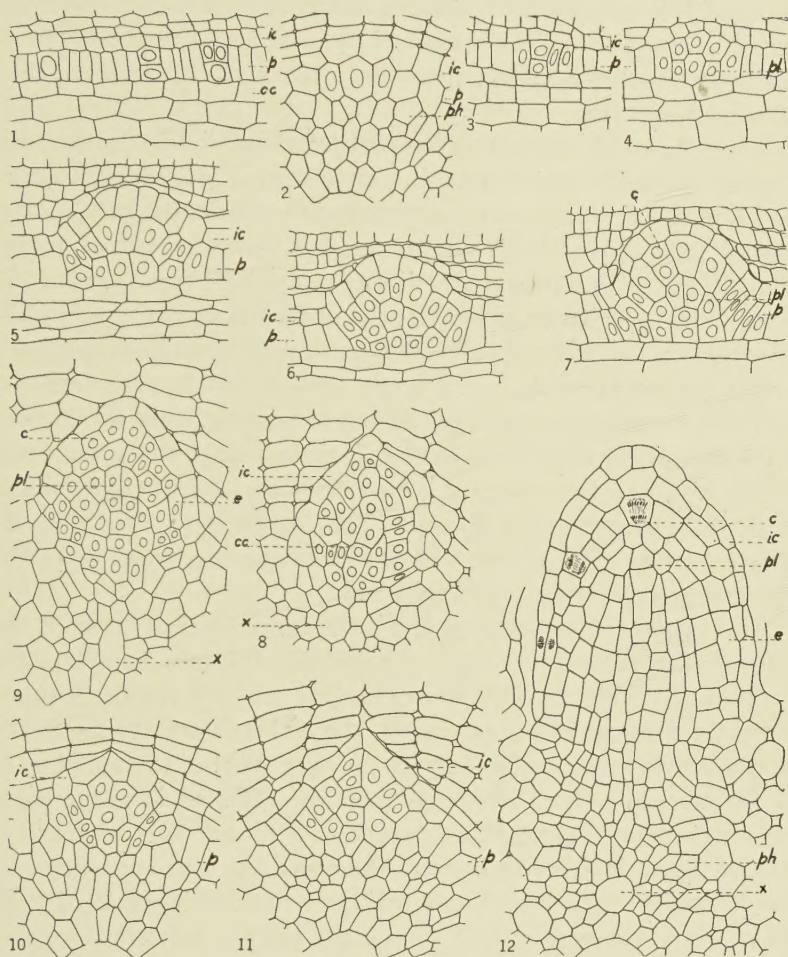
The roots were cut in paraffin 7 or 8 μ thick, and stained in the haematoxylin or in safranin with a counterstain. While cross-sections showed a greater number of sections of developing lateral roots, long sections were also necessary to form an idea of the true shape of the developing root and to get median sections well advanced, since the rootlets soon assume a downward direction within the mother root.

While the histogenic regions have already been determined, yet two things in the root of *Sagittaria* seem to deserve attention, the rise of the secondary root and the development of the intercellular spaces. Observations indicate that the primary, adventitious, and secondary roots all have the same histogenic regions: calyptrogen,

dermatogen and periblem in common, and plerome. This has been found to be a common condition in monocotyledons. While the regions of the root are easy to determine, their origins are rather more complex, each kind of root presenting its individual problem. Only the rise of the secondary root from the adventitious root will be discussed here.

The pericycle of the adventitious roots develops rapidly and gives rise to many rootlets, so that a longitudinal section of a root may show practically all stages of origin of secondary roots. It is difficult to determine the very first stage of rootlet development. The condition shown in fig. 1, in which the rootlet apparently develops from one pericycle cell, is occasionally seen; but the more common condition shows the enlargement of a plate of cells (fig. 2) before any periclinal division takes place. Even in this case the lateral cells must be involved, since no divisions of the upper and lower cells were found which would indicate increase in lateral bulk. Previous to the periclinal division of the pericycle cells, it is difficult to determine whether a cell division is to initiate a rootlet or merely to add to the length of the pericycle. It has not been decided, therefore, whether the rootlet is initiated by one cell or by a plate of cells; but if a plate of cells does initiate the rootlet, the center one is always larger and is at least one cell generation ahead of the surrounding cells, an advance which is maintained throughout all its future generations (figs. 3-12).

After a patch of pericycle cells has enlarged, the middle cell divides periclinally and then anticlinally, the surrounding cells dividing in the same way but later (figs. 3-7). JANCZEWSKI (2) states that "the root is almost always engendered by three pericyclic cells of which the two laterals constitute the cortex of the rootlet while the median cell cuts transversely into two parts, the lower of which becomes the central cylinder while the upper serves to complete the cortex." Judging from figs. 3-5, it seems apparent in this root that a group as many as five cells wide usually is involved in rootlet formation; that not only the middle cell but also its immediately surrounding layer of cells enters into the plerome; that the outer row of cells may add to the cortex; and that the top cells cut off give rise to cap, epidermis, and cortex. Also some sections (figs. 7, 8) would seem to indicate that the first periclinal division does not mark off the entire plerome,



FIGS. 1-12.—Fig. 1, longitudinal section of root tip showing three stages of rootlet development. Fig. 2, same in cross-section. Figs. 3, 4, longitudinal sections showing stages beyond fig. 1. Figs. 5, 6, longitudinal sections with inner cortical layer investing rootlet and showing breakdown of cortical tissue. Fig. 7, first cell of calyptragen in longitudinal section. Fig. 8, cross-section with axial row probably adding to cortex in addition to central cylinder. Fig. 9, cross-section with all regions of rootlet differentiated. Figs. 10, 11, mechanics of thrust of rootlet, cross-section. Fig. 12, advanced stage of rootlet, cross-section: *c*, calyptragen; *cc*, central cylinder; *e*, epidermis; *ic*, inner layer of cortex; *p*, pericycle; *ph*, phloem; *pl*, plerome; *x*, xylem. $\times 220$.

but that it is added to by further divisions of the top cell. Throughout the secondary root, the central cylinder usually remains three cells wide, with the middle row one to two cells in advance of the surrounding layer.

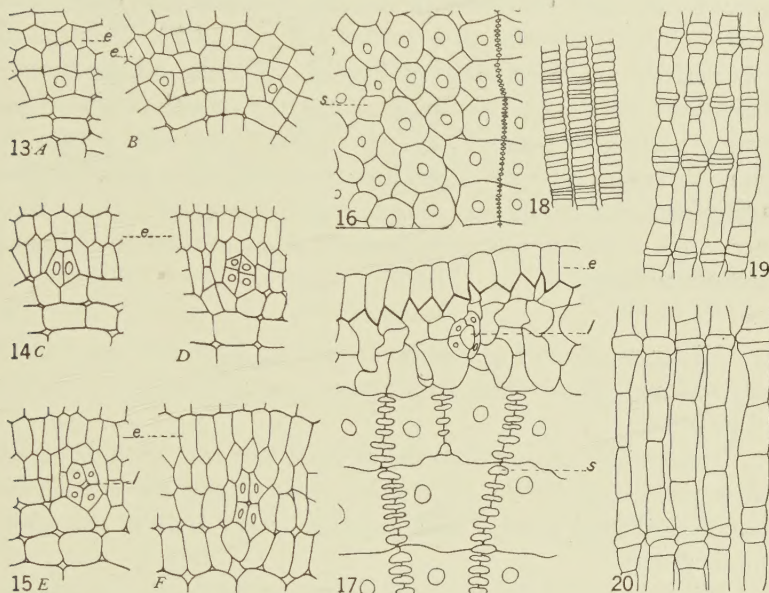
The cells which result from the first periclinal division of the pericyclic cells divide anticlinally, and after several generations, during which they have added to the cortex, give rise to the calyptrogen (fig. 9). The origin of this calyptrogen has been a matter of discussion, REINKE (3) claiming that it originates from that layer of the cortex which closely invests the rootlet during its development; while JANCZEWSKI (2) claims that it is differentiated from cells of pericyclic origin. Judging from fig. 12, it would appear that REINKE was correct, but a careful tracing of cell origins shows that while the cortical layer completely covers the rootlet, it adds only to the lateral bulk of the cap, and that the real calyptrogen comes from divisions of cells which are pericyclic in origin. The dermatogen arises after the calyptrogen is well defined, and has its origin in common with the cortex throughout the life of the plant.

The young rootlet, protected by the inner cortical layer of the mother root, assumes the shape of a wedge as it forces the cells of the cortex apart (figs. 10, 11). Since elongation of the mother root relieves the pressure above and below, the real resistance to the thrust of the growing rootlet is due to the pushing apart of the radial walls of the cortical cells. The root is therefore different in shape when seen in cross and in longitudinal sections. This may be seen by comparing figs. 6 and 10. Only after the rootlet is well advanced and the lateral pressure has ceased, owing to the development of large air spaces in the mother root, does it present a symmetrical form in all sections.

Beside the origin of the secondary root, the cortex presents some points of interest in the development of its intercellular spaces. The cortex of the root is added to from two regions, next to the central cylinder and just below the epidermis. As the root increases in diameter, the cells enlarge and intercellular spaces appear. These spaces are of two kinds, those which form air canals and those which carry latex.

The air spaces arise in the ordinary way by a breakdown, or by a

splitting of the middle lamella at the corners of the cells, a process which continues until the cells assume the form of a cross in all sections. As growth continues, these cells break down and there remain only partitions a cell wall thick between two or three live hypodermal layers and a few cortical layers immediately around the stele. This arrangement is periodically interrupted by layers of live cells which connect the outer and inner live layers.



FIGS. 13-20.—Figs. 13-15, stages in development of latex vessel in hypodermal layer of root; $\times 220$. Figs. 16, 17, stages in formation of intercellular spaces in radial walls of cortex; $\times 350$. Figs. 18-20, longisections of differentiation within cortex of alternate bands of short and elongated cells: *e*, epidermis; *l*, latex vessel; *s*, air space. $\times 220$.

In the development of the cortex, the differentiation of these connecting layers is early marked out. As the cortical cells increase in size, certain groups of them do not enlarge in the long axis of the root. Figs. 18-20 show these regularly occurring bands of narrow cells, which have small intercellular spaces. With continued growth of the cells these narrow bands become more noticeable. Cross-sections of the root show that for a while they enlarge with the diameter of the root, but seem to have lost their power of division. Continued

growth of the region next to the stele and of the hypodermal region stretch these cells. Then breaks occur in patches in the middle lamella, on the radial faces of the cells (figs. 16, 17); and the connecting strands are stretched more and more, until they may be as long as the cell is wide. They may even break without appearing to injure the cell, so far as staining reactions indicate.

The spaces which carry the latex arise in the second hypodermal layer, and are similar in development and appearance to resin ducts. A cell divides to give rise to a 5-sided cell (fig. 13 *B*). This cell divides radially and then tangentially (fig. 14). The middle lamella breaks down at the point of contact of the four cells thus formed and forms a continuous passage (fig. 15). These tubes arise within the region of the root cap and extend into the stem, where spaces having similar form and method of development are found. These latex spaces seem to suffer from crowding and a few are lost entirely as a result of crushing.

Summary

1. All types of roots of *Sagittaria latifolia* have the same histogenic regions: calyptrogen, dermatogen and periblem in common, and plerome.

2. The rootlets arising from the adventitious root probably come from a plate of pericyclic cells, since single origins show little evidence of anticlinal division adding to the lateral bulk of the meristematic group.

3. The plerome of the rootlet is probably differentiated with the first anticlinal division, but some sections indicate its later separation from the common meristematic group. The plerome arises as a plate of cells with the central cell more developed, and not from a single cell.

4. The inner layer of the mother root completely covers the tip of the rootlet and adds to its lateral bulk, but does not give rise to the calyptrogen.

5. The intercellular spaces of the cortex are of two kinds, gas spaces and latex canals. The gas spaces enlarge and break down most of the cortical cells. These spaces are interrupted by plates of live cells at right angles to the long axis of the root. These plates of cells are the only live connections between the hypodermal layers

and the stele, and develop peculiar rows of intercellular spaces on their radial faces.

6. The latex canals arise in the second hypodermal layer, and apparently are reduced in number by lateral pressure.

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